THE

AMERICAN NATURALIST

VOL. XXVIII. November, 1894. 335

THE MECHANICAL CAUSE OF FOLDS IN THE APERTURE OF THE SHELL OF GASTEROPODA.[1]

BY WM. H. DALL.

The folds which are frequently present on the columella and the lip of the aperture of the shells of Gasteropoda, may, I think, be traced to a mechanical cause. In considering the dynamic relations of the animal to its shell we may obtain satisfaction on this point. In the fusiform rachiglossa an anatomical difference exists to which I believe attention has not hitherto been called. Indeed, unless the principles of dynamic evolution are granted it is a difference which would appear to have little or no significance. These principles, however, afford a key which seems to unlock this and many other mysteries. In the plicate forms of this sort the adductor muscle, which in all gastropods is attached to the columella at a certain distance within the aperture, is attached *deeper within the shell* than in non-plicate forms. The point of attachment may be an entire turn, or even more, behind the aperture, while in short globose few-whorled shells and in the non-plicate forms it is, as a general rule, little more than half a turn within the aperture.

[1]Adapted from the Transactions of the Wagner Free Institute of Science, Philadelphia, Vol. III, 1890, p. 58.

Now let us consider the dynamics of the case. We have, reduced to its ultimate terms, a twisted shelly, hollow cone, sub-angulate or even channelled at two extremes corresponding to the canal and the posterior commissure of the body and outer lip. Inside of this we have a thin, loose epithelial cone, the mantle, of which the external surface especially toward the margin, is shell-secreting; lastly, inside of the mantle-cone we have a more or less solid third cone, consisting of the foot and other external parts of the body of the animal, which can be extended beyond the mantle-cone outwardly, as the mantle-cone can be beyond the shell-cone. The body-cone and the mantle-cone are attached at one of the angles of the shell-cone some distance within the opening of the spiral of the latter. The two outer cones constitute a loose, flexible funnel within a rigid, inflexible funnel, while the body-cone forms a solid, elastic stopper inside of all.

What will happen according to mechanical principles (which can be tested by any body with the simplest apparatus) when the mantle-cone is withdrawn into a part of the shell-cone too small for the natural diameter of the contracted mantle-cone? It must wrinkle longitudinally. Where will the wrinkles come? They will come at the angles of the shell-cone first; they will be most numerous toward the aperture, since toward the aperture the mantle-cone enlarges disproportionately to the caliber of the shell, owing to its processes, the natural fold of the canal, etc., etc.; the deepest and strongest wrinkles will be over the pillar, owing to the fact that the attachment of the adductor prevents perfect freedom in wrinkling, and the groove of the canal will mechanically induce the first fold in that vicinity. The most numerous small wrinkles will be near the aperture opposite the pillar, because of the mantle-edge this is the most expanded part, and there will be a tendency to a ridge near the angle of the posterior commissure. Repeated dragging of a shell-secreting surface, thus wrinkled, over a surface fitted to receive such secretion, will result in the elevated shelly ridges which on the pillar we call plications, and on the outer lip liræ, if long, or teeth if short. The commonly existing subsutural internal ridge on

the body of the shell near the posterior commissure will mark the special conditions in that part of the aperture.

When the secreting surface is thus wrinkled or corrugated longitudinally the wrinkles and the concave folds between them will be directed in the sense or direction in which the body moves in emerging from or withdrawing to the whorl. The summits of the convex wrinkles will be appressed more or less forcibly against the shell-wall exterior to them in which they are contained. The semi-fluid, living secretion of which the shell-lining is built up, exuding from the whole surface of the mantle, will be rubbed away from the lines of the summits of the wrinkles and tend to accumulate in lines corresponding to the concave furrows between the wrinkles. This secretion hardens rapidly, and these lines would become somewhat elevated ridges which would by their presence (when once initiated) tend to maintain the furrows and wrinkles in the same place with relation to the thus-initiated liræ, as these elevated lines are called when on the outer lip; or plaits, when situated on the pillar.

The modification referred to generally takes place during resting stages of the animals' growth, since while the animal is rapidly extending its coil the secretions seem to be concentrated along the mantle margin, while the general mantle-surface resumes its secretive function (or the latter becomes active) somewhat later, after the formation of a definite shelly varix, or thickened margin, indicating a resting stage in the animal's career. It is probable also that during rapid growth there is less compression of the tissues than during the resting stages. The external sculpture and some of the modifications of the aperture are connected with the functions of the extreme edge of the mantle; those we are at present considering relate more especially to the function of its general surface by which the layer which lines the whorls, the pillar, plaits and liræ are solely secreted and deposited.

In species with the adductor muscle attached to the pillar near the aperture the wrinkles would be fewer, and their action, if any, confined to the vicinity of the margin of the aperture. The deeper the attachment the greater will be the

compression of the secreting surface and the distance over which it is constantly dragged back and forth, and the consequent length of the ridges of shelly matter deposited. If the inner or mantle-cone had the whole cavity to itself, it is evident that it could and would infold itself in a manner which might not appress its folds against the inner surface of the rigid outer or shell-cone. But there the mass of the solid and elastic foot and external body comes into play, and by its withdrawal inward forces the wrinkled mantle-cone against the shell. The mantle is thus confined between a rigid outer and

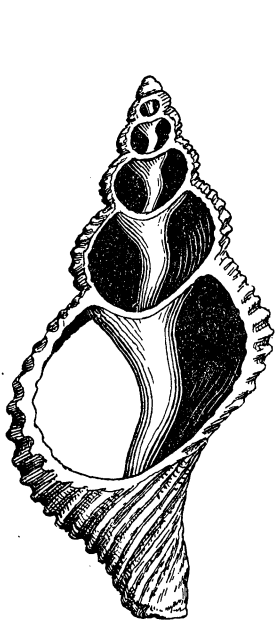

Fig. 1.

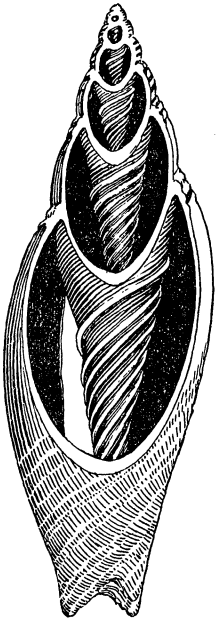

Fig 2.

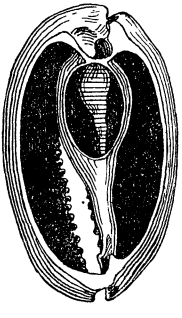

Fig. 3.

Fig. 1. *Fusus parilis* Conr. a gastropod in which the caliber of the spire contracts uniformly within the aperture but which, having a short retractor muscle develops no plications on the axis.

Fig. 2. *Mitra lineolata* Heilprin, a gastropod otherwise similar, but in which the retractor is long and deep seated and in which the axis becomes plicated.

Fig. 3. *Siphocypræa problematica* Heilprin, a gastropod in which the aperture is contracted and the cavity within ample so that plications are developed on the sides of the aperture but not on the axis within.

an elastic inner surface, with the result that it cannot recoil from the former and that a certain uniformity of size and direction is imposed upon the wrinkles, except where the recess of the canal allows them to become more emphatic, or to a less degree, the posterior angle permits a slight expansion. The mechanical principles involved may be readily illustrated by the experiment of pulling a handkerchief through the neck of a bottle, or funnel, followed by a cork in the center. Of course, the more nearly the apparatus conforms to the form and twist of a spiral shell the more nearly the results will approximate to those of nature. It is difficult, however, to find any artificial tissue which will correspond in elasticity, or capacity for partial self-contraction, to the living tissues concerned in nature. Hence an exact conformity is not to be expected though the mechanical principles may be reasonably well illustrated.

A comparison of specimens will show that the results exhibited agree with marvellous precision with the results called for by the preceeding hypothesis, based on the dynamical status of the bodies concerned, their motions and secretions. The agreement is so complete as to amount to a demonstration, though in certain cases there may be complications which need additional explanation.

A point which may be noted in regard to the Volutidæ, to which my attention was called by Mr. Pilsbry, is that in this group the mantle is greatly extended and there would be more of it to be wrinkled than in such forms as Buccinum, etc. It may be added that the forms in which we note the beginning of plaits for this family, many of them, such as Liopeplum and Volutomorpha, had the mantle so extended as to deposit a coat of enamel over the whole shell, as in the modern Cypræa, so that here we have an additional reason why plication should be emphasized in this group.

Of course, as before noted, the mechanical principles are the same in any group of gastropods, but among those in which the wrinkling is confined to the region of the aperture or those shells which are lirate or dentate as opposed to plicate, several other principles come into play which may be briefly referred

to in passing. In the first place, those species which have a very extended mantle, with hardly an exception have a lirate aperture (*Oliva, Olivella, Cypræa, Trivia,* etc.). With species in which there is a widely extended mantle and yet no lirations, it will usually be found that the mantle is not entirely withdrawn into the shell in such forms, or is permanently external to the shell (many *Opisthobranchiata, Marseniidæ, Sigaretus, Harpa,* etc.). In a group, like the *Cypræidæ,* where nearly all the species are lirate on both lips, there are a few which want these liræ, and these are species which have a wider aperture in the adult than most of the genus, and in which we should expect the wrinkles to be less emphatic.